

ULTRASTRUCTURE AND EARLY DIAGENESIS OF THE VISÉAN ALGA *KONINCKOPORA*

by V. PAUL WRIGHT

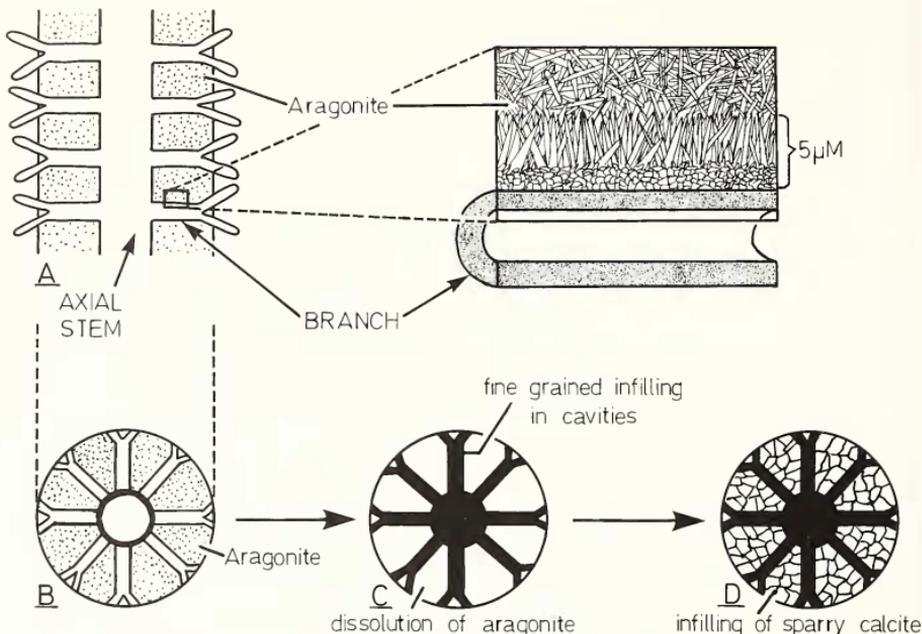
ABSTRACT. The problematical genus *Koninckopora* is one of a number of fossil dasycladacean algae which possess micritic microstructures. The microstructure of the carbonate which encrusted *Koninckopora* is compared with microstructures of other plant and invertebrate groups which are known to have transformed from aragonite to calcite. It is concluded that the encrusted parts of *Koninckopora* were originally composed of calcite not aragonite. *Koninckopora* thus differs from all living calcareous dasycladaceans and probably most fossil forms. It is suggested that the calcite that encrusted *Koninckopora* was a stable carbonate, that is, a low-magnesian calcite. Calcitic encrustation has developed on a number of occasions during dasycladacean evolution. The occurrence of an acicular wall in the so-called double-walled *Koninckopora* has previously been considered to be a primary biogenic structure. It is shown that this acicular layer is an early cement overgrowth. The presence of double-walled forms has been used erroneously as a biostratigraphical indicator in the Viséan.

THE original mineralogy of calcareous fossils is often assumed simply on the basis of comparisons with that of living counterparts. Many unusual fabrics in calcareous fossils are often passed over as the result of recrystallization or poor preservation. Recent suggestions that marine ooids in the Palaeozoic were composed of calcite and not aragonite as in modern ooids (Sandberg 1975a) highlights the dangers of making assumptions about primary mineralogies. A study of *Koninckopora* serves to illustrate the need for the careful analysis of ancient skeletal fabrics and to delimit primary biogenic and secondary diagenetic fabrics from one another.

Koninckopora is a poorly understood dasycladacean alga from the Lower Carboniferous (Viséan). It is geographically widespread, being found, for example, in rocks of this age from Newfoundland (Jansa, Mamet and Roux 1978), Tennessee (Rich 1974), Nova Scotia and Britain (Wood 1942), Belgium (de Koninck 1842), and Japan (Konishi 1956). The fossil was interpreted originally as a coral, and given the name *Calamopora* by de Koninck (1842). Lee (1912) believed it to be a bryozoan, and renamed it *Koninckopora*. Wood (1942) then carefully restudied the organism, reinterpreting it as a dasycladacean alga because of its mode of growth and morphology. He stressed its resemblance to the extant dasycladacean *Bornetella*. The taxonomy of the alga has been reviewed by Mamet and Roux (1975) and Jansa *et al.* (1978).

Most modern calcareous dasycladaceans produce aragonite as an encrustation around the thallus. Precipitation begins on and between the branches, which are arranged in whorls around a central stem and on the stem (text-fig. 1). On decay of the plant material, an aragonite tube with radiating pores is left. The pores connect the central cavity to the exterior, and are the sites of the branches during the life of the plant. Although this extracellular precipitation is the most common type met with in extant dasycladaceans, intracellular precipitation occurs in the distinctive alga *Acetabularia* (see Wray 1977) and in *Bornetella* (Valet 1968, 1969). Other mineral phases besides aragonite occur rarely, e.g. calcium oxalate in the reproductive discs of *Acetabularia* (Elliott 1979) and calcite (see below).

Wood (1942, p. 212) described the unusual appearance of the walls of *Koninckopora*, noting that they are composed of very fine grained calcite and not the typical coarse calcite replacement fabric seen in other fossil dasycladaceans. Although Recent calcareous dasycladaceans are composed of fine grained aragonite (Milliman 1974, p. 72), fossil forms are usually preserved in sparry calcite, which formed as mould fillings (Wray 1977, p. 91) deposited in voids left by the dissolution of the original aragonite (text-fig. 1). Bassoullet, Bernier, Deloffre, Genot, Jaffrezo, and Pognant (1977,



TEXT-FIG. 1. Ultrastructure and diagenesis of a typical calcified dasycladacean. A, longitudinal section showing the distribution of the aragonite encrustation; inset shows the typical ultrastructure of the encrustation. B, transverse section. C, early diagenesis includes post-mortem infilling of branch and axial cavities and later dissolution of aragonite. D, final stage infilling of solution voids by sparry calcite.

p. 159) have suggested that the calcite in *Koninckopora* may be original, rather than a secondary replacement of aragonite. Wood (1942, p. 212) also believed the microstructure to be original.

The aim of this study has been to investigate the microstructure of *Koninckopora* in order to ascertain its original composition and subsequent diagenesis.

Materials and methods of study. Samples of *K. inflata* from the Llanelli Formation, of Arundian (Lower Viséan) age, exposed at Daren Cilau, Llangattock, Powys, Wales (Grid reference SO 200 158) were examined. The fossils occur in a cross-bedded, oncolitic, calcareous sandstone. The occurrence of *K. inflata* at this locality was first noticed by George (1954). These samples were examined with the light and scanning electron microscopes; the original SEM stubs were inadvertently destroyed, but the original negatives together with thirteen rock chips from the same samples have been deposited in the National Museum of Wales (NMW) under Accession number 80.3G. Additional thin sections were obtained by courtesy of the British Museum (Natural History) (BM).

WALL STRUCTURE OF *KONINCKOPORA INFLATA*

K. inflata from Daren Cilau occurs as fragments, sometimes more than 12 cm long and 1 cm in diameter. The rock is a quartz sandstone with a calcitic cement, and the axial stem cavity of the algal tubes is filled with the same material as the rock matrix. The outer surface is usually covered by up to 2 mm of micrite; this coating is nearly featureless under the light microscope, although there are

TEXT-FIG. 2. Typical appearance of the walls of *Koninckopora inflata*; photomicrograph, $\times 80$. BM (NH) V23551, Tray Cliff, Castleton, Derbyshire.



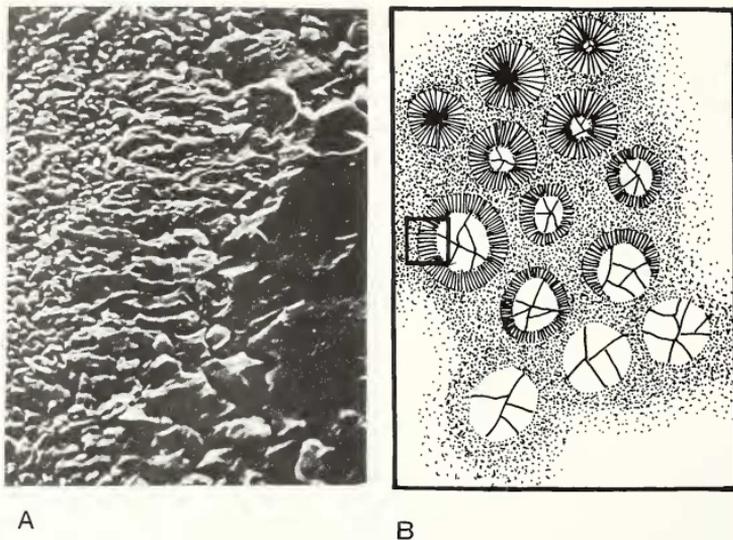
examples of the cyanophyte genus *Ortonella* Garwood in places. Under the light microscope, the walls of *Koninckopora* are micritic and it is not possible to distinguish grain shapes and orientations. The pores are filled with spar, having a grain size reaching $60\ \mu\text{m}$. The typical appearance in thin section is shown in text-fig. 2.

Under the SEM, the walls are seen to be composed of a randomly arranged equant to prismatic micrite and fine spar, with some irregular crystals. They vary from 1.0 to $10.0\ \mu\text{m}$ in diameter (text-fig. 3), with no pattern to the size variation. Rarely prisms occur which appear to have broken down into micrite (text-fig. 3).

Material in the walls acted as a substrate for the growth of acicular calcite, which is patchily



TEXT-FIG. 3. Detail of the wall of *Koninckopora inflata* showing micrite and a prismatic grain in the centre; SEM photograph, $\times 2120$, Daren Cilau.



TEXT-FIG. 4. A, detail of a branch cavity infill showing from left to right the micritic wall, acicular overgrowth, and sparry calcite; SEM photograph, $\times 1240$, Daren Cilau. B, diagram showing various stages of the infilling of branch cavities by acicular overgrowths; the diagram shows an oblique longitudinal section and has been drawn from a peel; the box indicates the position in A, $\times 100$, Daren Cilau.

distributed in the pores (text-fig. 4a, b). This acicular crust is composed of a single layer of needles averaging $20 \mu\text{m}$ in thickness, with individual needle widths of 2.0 to $4.0 \mu\text{m}$ (text-fig. 4a). Wood (1942, p. 214) noted that fibrous calcite was precipitated in the empty pores of *K. inflata* from Nova Scotia, before an early micrite coating (algal dust of Wood 1941), thus indicating early cementation. Samples from Daren Cilau do not show this feature.

Some pores contain calcite needles but few are completely filled with them; the remaining space is filled with fine to medium grained spar. Comparison of the material described by Wood (1942) with specimens from the Forest of Dean, show that the acicular cements in pores are of very early development. The patchiness of the acicular cement is not due to dissolution, for no signs of dissolution were observed on existing needles. The acicular cement crusts are very well preserved (text-fig. 5b). The crystals sometimes grew perpendicularly from the walls, some maintaining a constant width as they increase in length, and some form radiating fans with crystals widening outwards away from the wall.

Two other cement types occur. In material from Ireland and Nova Scotia, contained in Wood's collection at the British Museum (Natural History), both radiaxial fibrous calcite (Bathurst 1971, 1975, p. 426; Kendall and Tucker 1973) and radial fibrous spar (Bathurst 1975, pp. 484, 485) can be found. Both appear in the axial cavity of the alga, but not in or between the branch cavities.

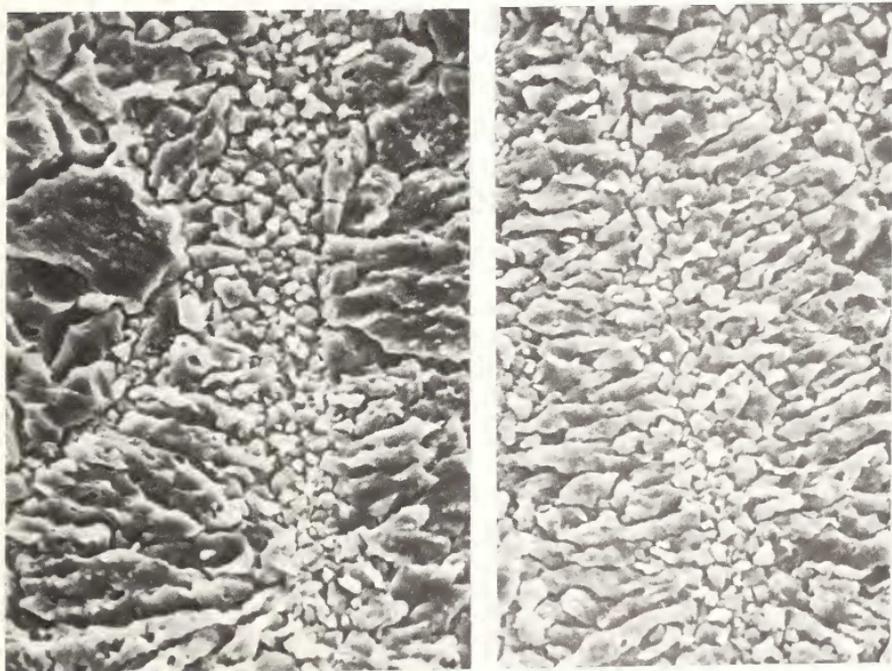
DISCUSSION

The majority of fossil dasycladaceans are preserved as cavity-fill spar, the result of the filling of voids created by the dissolution of aragonite. *K. inflata* differs in ultrastructure, both from this and from Recent dasycladaceans as described by Flajs (1977a, b) and Borowitzka, Larkum, and Nockolds

(1974). These authors described structures which consist largely of orientated and random needles of aragonite. If the walls of *Koninckopora* had been composed originally of aragonite, its replacement by calcite must have followed some pathway other than the dissolution and void-fill seen in most other fossil dasycladaceans.

Another such pathway has been described in detail by James (1974). In this transformation pathway a very thin solution film dissolves the original aragonite from corals in meteoric ground water zones. This thin film dissolution process leaves ghosts of the original fabrics (calcitization of Bathurst 1975). The resulting calcite structures consist of quite coarse grained calcite, with ghosts, often outlined by organic matter, of the original structures (e.g. see Dodd 1966; Gavish and Friedman 1969; Talbot 1972; James 1974; Pingitore 1976). The preservation seen in *Koninckopora* is very different from that resulting from this process. There are no ghosts, and the grain size is generally micritic.

Purdy (1968, p. 149) has argued for the transformation of aragonite to calcite as 'texturally non-destructive', occurring via a process of extremely fine scale solution-precipitation. He quotes the preservation of micrite envelopes in ancient limestones as an example. These envelopes are usually aragonitic in Recent examples, but are calcite in the older rocks. The micritic texture is preserved during alteration of the unstable mineral. Bathurst (1975, p. 334) suggested that organic materials



A

B

TEXT-FIG. 5. A, longitudinal section showing micritic wall (centre), radiating overgrowth (lower left), and wall-sparry calcite contact (upper right). B, longitudinal section showing detail of the acicular overgrowths on either side of a micritic wall; both SEM photographs, $\times 1000$, Daren Cilau.

within the envelopes may have acted as a template during transformation, restricting the size of the diagenetic calcite. This is very similar to the proposition of Shearman, Twyman, and Karimi (1970) for the preservation of radial-fibrous fabric in ancient ooids.

This organic template process seems unsuitable as an explanation for the small grain size of the calcite in *Koninckopora*. Sandberg (1975a) has criticized the hypothesis, considering that if it operates in ooids, then it should do so in molluscs. Molluscan shell replacement shows no evidence of any such template, despite the presence of organic materials in the aragonitic layers. In addition, Recent calcified chlorophytes have no obvious organic matrix in their carbonates (Borowitzka *et al.* 1974; Wilbur, Colinvaux, and Watabe (1969).

There are a number of well-documented occurrences of biogenic aragonite replaced by micritic, low-magnesian calcite. Such replacements in Recent and fossil material have developed under unusual diagenetic conditions (Scherer 1975, 1977) and cannot explain the widespread occurrence of *Koninckopora*.

From such considerations it is concluded that the walls of *Koninckopora* did not originally consist of aragonite, but were calcitic. Calcite has been recorded from Recent chlorophytes: Wood (1942, p. 212) found calcite in the dasycladacean *Bornetella nitida* Munier-Chalmas, and Borowitzka and Larkum (1976, p. 867) have reported it from the codiacean *Halimeda*. The latter occurrence seems to be a cement growth on the primary aragonite, found only on the older parts of the plant (Borowitzka, pers. comm. 1978). Calcite has also been reported from *Penicillus*, but this requires confirmation (Milliman 1974, p. 72).

None of these authors give the composition of the calcite that they report, and that of *Koninckopora* may have been low or high in magnesium. The other algal divisions are no guide here, since high-magnesian calcites occur in the Rhodophyta (6–23 mole % $MgCO_3$) and low-magnesian varieties in the cyanophytes, charophytes, and chrysophytes (2–3 mole % $MgCO$) (Bathurst 1975, p. 236). Thus *Koninckopora* may have been encrusted with calcite which was low, intermediate, or high in magnesium.

A high-magnesian calcite precursor

Little information is available on the ultrastructural effects of the transformation from high- to low-magnesian calcite. Sandberg (1975b, p. 589) has described such changes in bryozoans; they are extensive, the final ultrastructure bearing little resemblance to the original high-magnesian calcite-aragonite skeleton. The diagenetic fabric, in most cases, consists of elongate crystallites orientated perpendicularly to the original wall surfaces, although irregular granular mosaics also occur. This fabric, derived from a mixture of unstable minerals and heavily influenced by the animal itself, is unlikely to develop from the presumably monomineralic, essentially inorganically produced (see Borowitzka *et al.* 1974) dasycladacean carbonate, even if it were high in magnesium.

Low-magnesian calcite

If the *Koninckopora* samples which have been examined had possessed a more elaborate and delicate ultrastructure, it might indicate a primary origin for the fabric. In that case, the original carbonate would be the stable polymorph, a low-magnesian calcite. The fabrics formed by this mineral, as found in other algal divisions such as the Cyanophyta (Riding 1977; Monty 1976) and the Chlorophyta (Borowitzka *et al.* 1974, p. 197; Golubic and Fischer 1975) are variable. Most members of these groups when calcified are composed essentially of inorganically precipitated carbonate, the plants having little or no influence over the fabrics produced, as is seen in living dasycladaceans. No characteristic ultrastructural fabrics occur which could be compared to *Koninckopora*.

It may be that *Koninckopora*'s ultrastructure is the result of recrystallization from an original low-magnesian calcite. There are various aspects of the ultrastructure which suggest that this is not the case. These may be taken to indicate that the ultrastructure has not resulted from any transformation which involved significant ultrastructural changes. The variations in crystal size and shape within the walls, and the presence of prismatic crystals, might be taken to argue against any extensive blanketing

recrystallization. The wall margins, unless showing overgrowths, are distinct. The acicular overgrowths arise from micrite in the wall quite uniformly, and their relationship shows no disruption by later recrystallization (text-fig. 5*a, b*). The width of overgrowth needles is very similar to the average diameter of the micrite crystals in the walls (which may indicate that recrystallization did not take place after the overgrowth formed). The latter two points in particular seem to indicate that little recrystallization has occurred in the walls.

If extensive low magnesian calcite recrystallization had taken place, the delicate acicular overgrowths would most likely have been structurally altered. These acicular crystals are evidence of the precipitation of a stable form of calcite associated with *Koninckopora*. However, Towe and Hemleben (1976) have shown that there is no textural alteration, even at electron-microscopy level, during the loss of magnesium in fossil miliolacean foraminifera. This raises the possibility that *Koninckopora* could have precipitated high-magnesian calcite.

Recently, Richter and Füchtbauer (1978) have suggested that the iron content of ancient skeletal carbonates is a guide to their original mineralogical composition. Skeletal structures which are preserved solely as non-ferroan calcite are considered by Richter and Füchtbauer to have undergone no diagenetic alteration and were therefore originally low-magnesian calcite. The *Koninckopora* material I have examined has, in all cases, been composed of non-ferroan calcite, as are the acicular overgrowths.

Many calcites, having stabilized from a high-magnesian calcite precursor, contain microdolomite inclusions (see Lohmann and Meyers 1977). Such inclusions have not been detected in any of the specimens studied from Daren Cilau, or from the British Museum collections. Furthermore, *Koninckopora* does not display preferential dolomitization, in contrast to skeletal carbonates composed originally of high magnesian calcite which often exhibit such preferential dolomitization (Buchbinder and Friedman 1970).

From the above, it is concluded that the walls of *Koninckopora* were probably calcitic rather than aragonite, and it is likely that this calcite was a relatively stable form, i.e. a low-magnesian calcite. The walls of the alga seem to have undergone very little post-depositional alteration.

There is a possibility that some other mineral, for example calcium oxalate, may have occurred in the walls of *Koninckopora*, as has been suggested recently for the unusual preservation of opercula in the Jurassic alga *Stichoporella* (Elliott 1979). With the limited information available on calcium oxalate, it is not possible to consider such a precursor at present.

Other fossil dasycladaceans with micritic microstructures

Besides *Koninckopora*, several other fossil dasycladaceans possess micritic walls. Bassoulet *et al.* (1977, p. 159) have drawn attention to *Koninckopora* and *Salpingoporella sellii* (Crescenti) Bassoulet, Bernier, Conrad, Deloffre, and Jaffrezo 1978 in this connection. Elliott (1978 pers. comm.) has pointed out the unusual thin-section appearance of *Pseudovermiporella* Elliott 1958. Rich (1974) described *Koninckoporoides monteaglenensis*, also with a micritic microstructure. Some of these forms have been assigned to groups other than the Dasycladaceae, probably because of their unusual microstructures. Korde (1966), for example, tentatively assigned *Pseudovermiporella* to the Rhodophyta, suggesting that its black colour in thin section was due to microstructure, biological habitat, and burial conditions, Elliott (1958) having originally remarked on the anomalous structure of the genus. From these reports, and the investigation of *Koninckopora* described here, it would appear that dasycladaceans with calcitic encrustations were more common in the past than has previously been suspected.

The *Koninckopora* material examined has come from a variety of lithologies representing quite different depositional conditions. It is unlikely that *Koninckopora* represents an alga which inhabited some unusual environment which caused its anomalous calcification. The conditions that induced the unusual fabric of the walls were widespread, and not merely of local importance, suggesting therefore that the unusual calcification was biologically controlled by the alga itself.

Recognition of early cementation

Many workers, for example Rich (1974), Mamet and Roux (1975), and Jansa *et al.* (1978), have described forms of *Koninckopora* with an acicular (fibrous) inner wall. Despite Wood (1942) showing that this acicular layer was an early cement, it has been described as a primary biogenic feature by later workers. Three lines of evidence suggest that these acicular layers are not a primary feature of the calcified structure. Firstly, the crusts are patchily distributed in any one specimen, and where they are absent there is no evidence of any dissolution. Secondly, in many specimens (text-fig. 4*b*, and Mamet and Roux 1975, pls. 4, 6) the acicular layer completely fills the pores. If this inner layer were of primary biogenic origin, it would have grown into the branch tissue, eventually severing the branch. Lastly, the calcification pattern of modern dasycladaceans shows a change from micritic near the branch margin to acicular in the pores (Flajs 1977*b*), which is the opposite to that seen in *Koninckopora*.

Such patchy intraskeletal cementation in the branch cavities and occasionally in the axial stem cavity, but without intergranular cementation on the exterior of the fossil, is commonly seen in modern carbonate environments (Bathurst 1975, p. 364). Such cements often match the composition of the host grain, as appears to have been the case with *Koninckopora*. The presence of an acicular wall is therefore purely a consequence of a suitable microenvironment within a branch cavity for the growth of cement. The use of *Koninckopora* with a second wall as a biostratigraphical marker for V_2a of the Viséan (Conil, Lys, Paproth, Ramsbottom, and Sevastopulo in press) must be seriously questioned. Indeed, any taxonomic division based on the occurrence of this second wall must also be questioned.

Dr. J. P. Bassoulet has informed me that the modern dasyclad *Bornetella oligospora* Solms-Lauback has an acicular aragonite layer developed on the inner surface of the branch walls. This has been described briefly by Valet (1968, 1969). Although this internal calcification pattern is reminiscent of *Koninckopora*, the considerable variability in the width of the acicular layer within the specimens of *Koninckopora* I have examined is unlikely to have developed as a primary biogenic feature and contrasts with that seen in *Bornetella oligospora*.

CONCLUSIONS

The ultrastructure of *K. inflata* Lee indicates that the organism encrusted with calcite, as suggested by Wood (1942), and not with aragonite. It has yet to be established whether the calcite was high or low in magnesium. Some other exceptional fossil dasycladaceans seem to have had similar properties, and may help with this problem, which highlights the problems of assuming the primary composition of fossil calcareous skeletal minerals simply on the basis of the composition of living counterparts. Specimens of *Koninckopora* from a number of areas exhibit similar early post-mortem cementation. These acicular cements have been considered to be part of the fossil structure. The development of an acicular inner layer has been mistakenly used as a biostratigraphical marker in the Dinantian for the base of V_2a . Stratigraphical subdivisions based on the appearance of double-walled forms appear suspect and should be reconsidered.

Acknowledgements. This work benefited from the assistance and interest shown by Corinne Danielli (Dept. of Botany, University College, Cardiff) who operated the SEM and critically read earlier drafts of the paper. I also thank Dr. G. F. Elliott of the British Museum (Natural History), for providing references, arranging loans of Museum specimens, and reading the manuscript, and Drs. J. A. D. Dickson (Nottingham) and Robert Riding (Cardiff) for constructively criticizing an earlier draft. The following people kindly gave advice and comments during the preparation of this paper: Dr. J. F. Danielli (Worcester Polytechnic Institute, Massachusetts), Professor R. G. C. Bathurst (Liverpool), Dr. W. H. C. Ramsbottom and Mr. D. Mundy (Institute of Geological Sciences, Leeds), Dr. J. P. Bassoulet (Paris), Professor R. Conil (Louvain), and Professor B. Mamet (Montreal). Mr. Rolf Jones (Dept. of Metallurgy and Materials Science, Cardiff) gave invaluable assistance with the electron microscope. S. Kershaw and D. G. Hilton prepared the text figures and Mrs. P. A. Privett typed the manuscript. The work was carried out while the author was in receipt of an in-service training grant (from the Mid Glamorgan Education Authority) which is gratefully acknowledged.

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Manuscript received 6 November 1979

Revised manuscript received 31 January 1980.